THE EVOLUTIONARY HISTORY OF THE PICTUS GROUP OF THE CRAYFISH GENUS *PROCAMBARUS* (DECAPODA, ASTACIDAE)

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The genus *Procambarus,* one of the nine genera of the holarctic family Astacidae, is represented in North America by approximately 100 species and subspecies. Sixteen of these occurring in the extreme southeastern part of the United States have been referred to collectively as the *Pictus Group* (Hobbs, 1942 : 129). The range of the group extends from the southeastern part of North Carolina southwestward to the central portion of the Florida peninsula and westward in the Florida panhandle across the Apalachicola River.

Among these sixteen recognizable forms are found some of the most generalized and some of the most highly specialized crayfishes of the North American continent. The ten more generalized species, composing the Pictus Subgroup, are inhabitants of streams in the lower piedmont and coastal plain throughout much of the range of the Group (Map 1). The six more divergent members of the group are equally distributed (Map 2) in the subterranean waters of Florida and in lentic and sluggish lotic surface waters of the coastal plain from North Carolina to Florida.

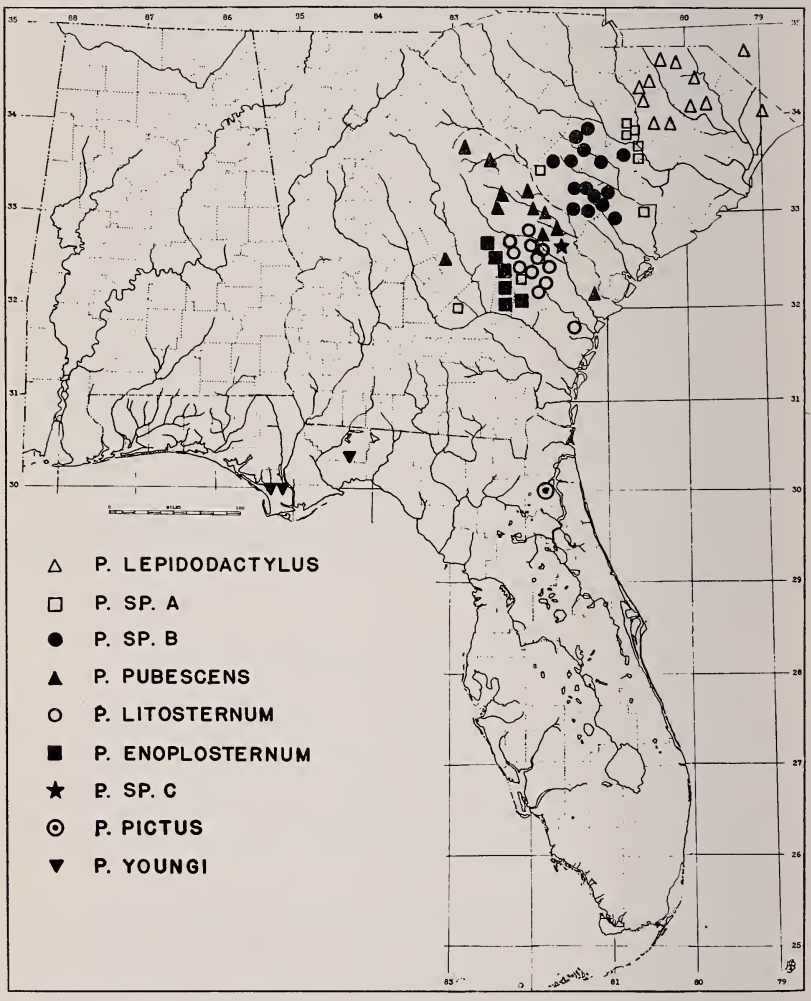
A summary of the inter-relationships and ranges of these sixteen species is presented here, with a discussion of the possible evolutionary history of the group.

Phylogenetic Position of the Pictus Group

It is not within the scope of this review to present an argumentative analysis of the nature of primitive characteristics in the members of the subfamily Cambarinae; however, certain basic assumptions must be stated prior to a discourse on phylogenetic trends that are supposed to have occurred in the ancestral lineage of the species concerned.

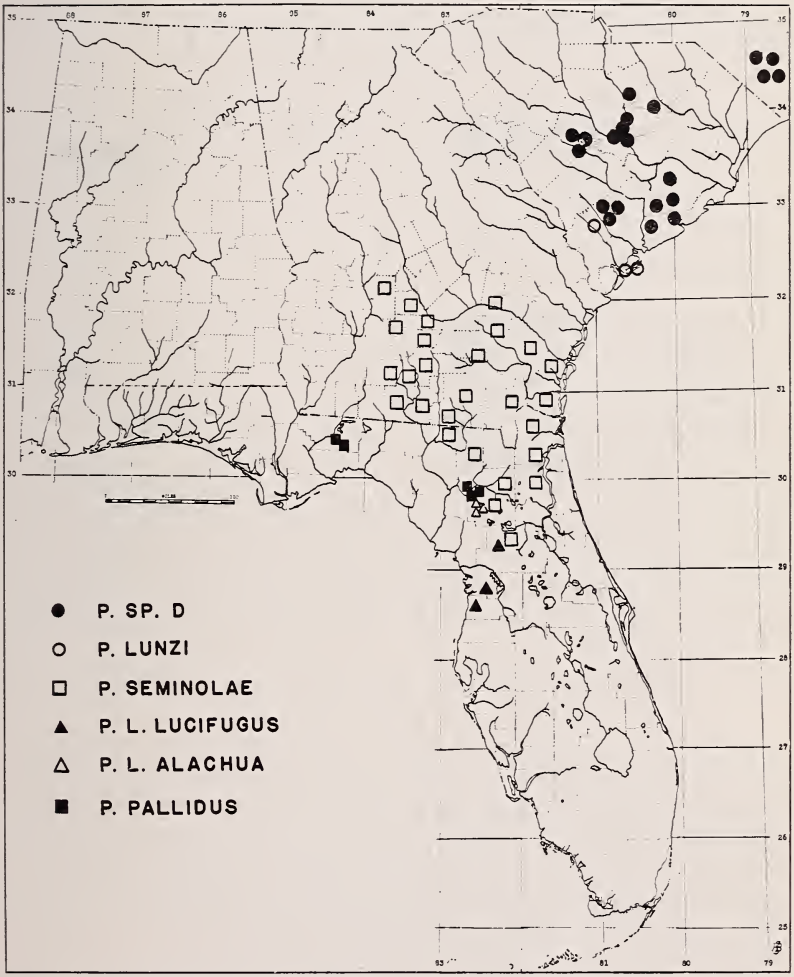
There are a number of reasons why this assemblage is here considered to comprise some of the most primitive members of the subfamily Cambarinae, and from them four are chosen for brief discussion.

A *broad, short areola* (not more than four times as long as broad, and its length not exceeding thirty per cent of the total length of the carapace) in contrast to a narrow, long one is here deemed more generalized. Such an assumption is in accord with the characteristics of the more generalized members of the other groups of the genus, as well as with those of more distant relatives in the family Astacidae.



Map 1. The distribution of the members of the Pictus Subgroup.

On the assumption that ornamentation, in the way of spines and color patterns, is more readily lost than gained in almost precisely the same arrangement or pattern, it is assumed that a *rostrum with subparallel or convex margins and bearing a pair of marginal spines* (figure 3) is a more generalized type than one in which the margins converge or are lacking spines altogether. It is known, for instance,



Map 2. The distribution of the members of the Seminolae and Lucifugus subgroups.

that the young of *Cambarus latimanus* in many localities have rostra with subparallel margins bearing lateral spines but that the adults in many areas lack such spines. This has also been observed in one of the undescribed members of the Pictus Group.

The *first pleopod of the first form male terminating in four distinct elements* is considered to be more primitive than one terminating in fewer elements since a repeated loss or reduction of one or more of them seems more probable than an erratic reapparance, in the same position, of such outgrowths.

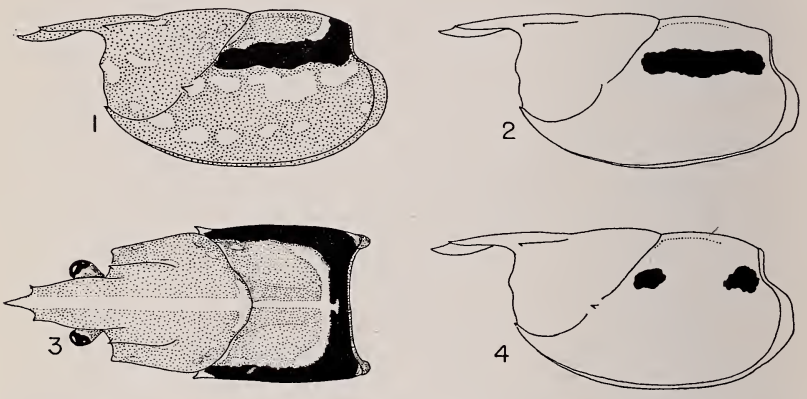


Figure 1. Lateral aspect of the carapace of *P. pictus* showing the sinistral *horn* and sinistral half of the *bar* of the saddle (in black).

Figure 2. Lateral aspect of the carapace of *P.* sp. D showing the reduced saddle with only the *horns* (only the sinistral one evident).

Figure 3. Dorsal aspect of the carapace of *P. pictus* showing the entire *saddle* (in black).

Figure 4. Lateral aspect of the carapace of *P.* sp. C showing only the two lateral *spots*, remnants of the sinistral *horn*.

A *color pattern* (figures 1 and 3) *which includes a U-shaped "saddle" on the thoracic portion of the carapace* is considered to be more generalized than one that has only portions of the saddle. This saddle is not restricted to the more generalized members of the Pictus Group but is also found in other crayfishes. "Spots" or "bars", representing segments of the saddle, are found in forms that are considered to be less primitive.

Other characteristics may be mentioned; however, these will suffice in the present discussion. Inasmuch as all four of these characteristics are found together in certain members of the Pictus

Group, those species are accepted as more closely approximating the ancestral stock of the Group than are those which do not combine them, and it is my opinion that this stock was, in all probability, ancestral to the entire genus *Procambarus*, if not to all the members of the Cambarinae.

Range of the Group

As stated in the introductory paragraphs, the range of the group extends from the southeastern part of North Carolina southwestward to the central portion of the Florida Peninsula and westward in the Florida panhandle across the Apalachicola River. In relation to the genus *Procambarus* as a whole, it occupies what almost amounts to the southeastern periphery of the range. Furthermore, the range is not a continuous one (Maps 1 and 2). Although collections have been made throughout most of the region between the known extremities, there appear to be gaps that are not readily explainable. For instance, there are no truly lotic members of the group in the triangular area between the Altamaha River in Georgia and the St. Johns and St. Marks rivers in Florida. Certainly the rivers and their tributaries in this area are similar to streams from which members of the group have been collected, and the absence of representatives of the Group in these streams is difficult to explain. Another obvious gap in the range, which I have been unable to explain, is the absence of a lentic species in the area between the Altamaha and Savannah rivers. Except for these two "ecological vaccua" in relation to the Pictus Group, the range cannot be said to be discontinuous.

Affinities Within the Group

Within the assemblage of crayfishes assigned to the Group there seem to be three distinct subgroups which are distinguishable both on anatomical and ecological bases. The most easily recognizable are the subterranean members, all of which are albinistic. This, the Lucifugus Subgroup, comprises two species, one of which is represented by two geographic races. The Pictus Subgroup consists of 10 species which seem to be restricted to permanent lotic situations. The Seminolae Subgroup comprises three species that frequent lotic and lentic, temporary and permanent bodies of water.

The Pictus Subgroup.—Of the ten species that belong to this subgroup all except three have been described, and these are here referred to as *Procambarus* sp. A, *Procambarus* sp. B, and *Procambarus* sp. C. These crayfishes all have short, broad areolae, and the males possess a first pleopod terminating in three or four distinct terminal elements; in most of them the margins of the rostrum are convex, subparallel, or slightly convergent, and all bear a pair of marginal spines; the color pattern is quite variable, but all have the entire "saddle" or portions of it.

Geographically the range of this subgroup is almost identical with that of the group, extending from tributaries of the Pee Dee River in southeastern North Carolina southward to Florida. There are no representatives of the subgroup in the triangular area between the Altamaha River in Georgia and the St. Johns and St. Marks rivers in Florida.

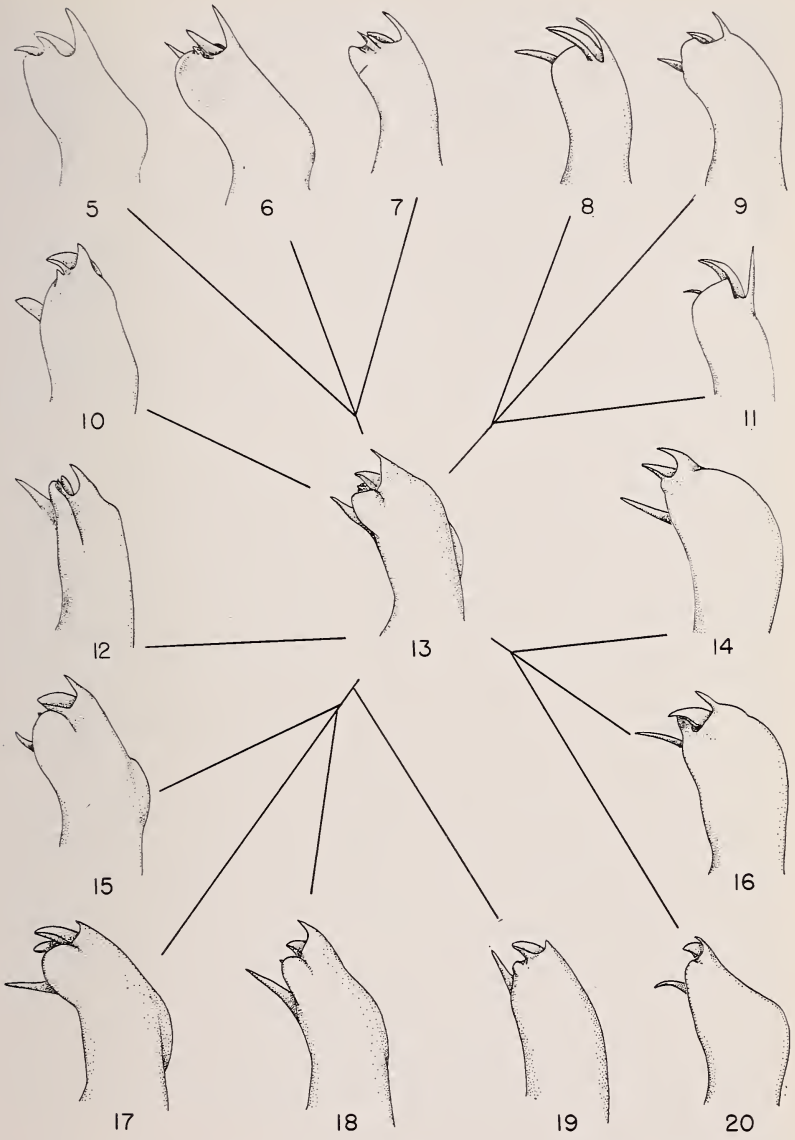
The ecological requirements of all of them seem to be satisfied in streams (mostly sand-bottomed) of the lower piedmont and coastal plain. The size of the stream, as well as the condition of the water, whether clear, silt-laden, or coffee-colored, appear to have no effect on the subgroup as a whole. Whether or not certain species may be limited by these factors remains to be demonstrated. There seems to be little doubt that a lotic habitat is necessary. These species occur abundantly in beds of *Vallisneria* and other aquatic plants. They also are found in litter and roots along the undercut banks of streams.

Procambarus lepidodactylus Hobbs (1947b : 25) has been collected from stream tributaries of the Pee Dee, Black, and Wateree rivers in the lower piedmont and coastal plain of South Carolina, and in extreme southeastern North Carolina.

Procambarus sp. A occurs in stream tributaries of the Wateree, Congaree, Edisto, and Savannah rivers in South Carolina, and from two apparently isolated localities in the Ogeechee and Ocmulgee rivers in Georgia.

Procambarus sp. B is found in stream tributaries of the Edisto, Salkehatchie, and Savannah rivers in South Carolina.

Procambarus pubescens (Faxon) (Faxon 1884 : 109) is known from stream tributaries of the Savannah, Ogeechee, and a single locality in the Altamaha river systems in Georgia.



Figures 5-20. Lateral views of terminal portions of first pleopods of first form males. 5. *P.* sp. B; 6. *P. pubescens;* 7. *P. youngi;* 8. *P.* sp. D; 9. *P. lunzi;* 10. *P. lepidodactylus;* 11. *P. seminolae;* 12. *P. litosternum;* 13. *P. pictus;* 14. *P. lucifugus lucifugus;* 15. *P. enoplosternum;* 16. *P. lucifugus alachua;* 17. *P.* sp. B; 18. *P.* sp. A; 19. *P. angustatus;* 20. *P. pallidus.*

Procambarus sp. C is known from a single stream tributary of the Ogeechee River in Screven County, Georgia.

Procambarus enoplosternum Hobbs (1947a : 5) frequents the stream tributaries of the Ohoopee River (tributary of the Altamaha River) in Georgia.

Procambarus litosternum Hobbs (1947a : 9) is known from the Canoochee, Ogeechee, and Newport rivers in Georgia.

Procambarus pictus (Hobbs) (Hobbs 1940a : 419) has been collected from a number of tributaries of Black Creek (tributary of the St. Johns River) in Clay County, Florida.

Procambarus youngi Hobbs (1942 : 131) is known from the St. Marks River, Leon County, Florida, and from a tributary of the Chipola River and from Wetappo Creek—the latter two in Gulf County, Florida.

Procambarus angustatus (LeConte) (LeConte 1856 : 401) is known only from the single type specimen in the Philadelphia Academy of Natural Sciences. The type locality cited by LeConte is exceedingly vague: "*Habitat in Georgia inferiore, in aquae purae rivalos qui inter colloculos arenosus* [sand-hills] *currunt.*" Efforts to find additional specimens of this distinct crayfish have thus far failed, and consequently no further reference is made to it in this discussion.

The characteristics of these species are summarized in Table 1 and figures 5, 6, 7, 10, 12, 13, 15, 17, 18, 19.

The Seminolae Subgroup.—Three species of the Pictus Group are united here because of their similar morphology and ecological distribution. One of the three has not been described and is herein designated as *Procambarus* sp. D. These crayfishes in general have narrower areolae than do most of the members of the Pictus Subgroup; the first pleopod terminates in only three distinct parts; the margins of the rostrum are convergent, and occasional specimens are found in which the marginal spines are reduced or absent; the color pattern is somewhat variable, but the "lateral horns of the saddle" are present or are represented by two pairs of dots as in figures 2 and 4.

The range of the subgroup extends from the lake region in southeastern North Carolina throughout the coastal plain (except between the Savannah and Altamaha rivers in Georgia), and on some of the coastal islands of South Carolina to Marion County, Florida.

Table 1. Summary of the characteristics of the members of the Pictus Group.

	Pictus Subgroup (Lotic Habitats)										Seminolae Subgroups (Lentic Habitats)			Lucifugus Subgroup (Subterranean Habitats)		
	P. angustatus	P. enoplosternum	P. lepidodactylus	P. litosternum	P. pictus	P. pubescens	P. youngi	P. sp. A	P. sp. B	P. sp. C	P. lunzi	P. seminolae	P. sp. D	P. l. lucifugus	P. l. alachua	P. pallidus
Areola lgth. / Carapace lgth. x 100	28.6	26.0—29.0	28.0—29.0	27.0—28.5	25.5—27.5	26.0—28.0	25.0—30.0	26.0—28.0	25.5—30.0	28.0—30.5	32.0—34.0	28.0—30.0	34.0—35.5	38.0—40.0	37.0—39.0	38.0—43.0
Areola lgth. / Areola width.	4.2	4.5—5.0	3.3—5.2	3.0—4.5	2.5—3.1	2.5—3.5	3.0—3.5	2.8—4.0	2.5—3.5	4.0—5.0	5.5—6.2	4.7—5.2	4.8—9.0	27.0—30.0	10.4—16.0	25.0—36.0
Rostrum	P	T	T	T	C-T	T	P	P	C-T	T	T	T	T	C	P-T	T
Color Pattern (Saddle)	?	s,B	B	s,B	S	wS or s,B	S	s,B	wS or s,B	H	s	s	H	A	A	A

A—albinistic; B—bars of saddle; C—convex margins; H—horns of saddle; P—parallel margins; s—two pairs of spots representing portions of horns; S—complete saddle; T—margins tapering toward apex; wS—saddle present but not sharply defined.

Representatives have not been reported from the panhandle of Florida.

The members of this subgroup frequent streams (usually the very sluggish areas), ponds, lakes, swamps, and roadside ditches. Too, they are found both in permanent and temporary bodies of water provided the watertable recedes not more than a few feet below the surface. They frequently dig simple, straight or gently slanting burrows, but seldom are the chimneys well-formed. Thus, these three species have a broader ecological tolerance than do the members of either of the other two subgroups. In spite of this, there are reasons to believe, as will be pointed out below, that they have been derived from a stock that resembled more closely the members of the Pictus Subgroup.

Procambarus sp. D ranges from Columbus and Bladen counties, North Carolina, in the lowermost portions of the piedmont and in the coastal plain to the Santee River system in South Carolina.

Procambarus lunzi (Hobbs) (Hobbs 1940b : 1) has been found in Hampton County, South Carolina and from several of the coastal islands in Beaufort County.

Procambarus seminolae Hobbs (1942 : 142) occupies a broad range from the Altamaha River, Georgia, southward to Marion County, Florida.

The characteristics of these species are summarized in Table 1 and figures 8, 9, 11.

The Lucifugus Subgroup.—Three of the six albinistic species reported from Florida belong to the Lucifugus Subgroup. All three have long, very narrow areolae; the first pleopod terminates in three or four well-defined elements; the margins of the rostrum are either convex, subparallel, or convergent and may or may not bear well-defined marginal spines; color is absent except occasionally for a straw brown shading on the abdominal terga of *P. lucifugus alachua.* It is only in this latter subspecies that any trace of pigment remains in the eyes.

The range of the subgroup is confined to Florida where it extends from Hernando County northward to Columbia County, and two localities are known in Leon County.

All three of these are confined to the subterranean waters and are found only in caves, sinkholes that reach the water table, and in an occasional well.

Procambarus lucifugus lucifugus (Hobbs) (Hobbs 1940a : 398) is known from only two caves, one each in Hernando and Citrus counties, Florida.

Procambarus lucifugus alachua (Hobbs) (Hobbs 1940a : 402) is known from a number of caves and sinkholes in the western part of Alachua County, Florida. Specimens that are somewhat intermediate between these two subspecies have been collected in Marion County.

Procambarus pallidus (Hobbs) (Hobbs 1940a : 394) has been taken from caves and sinkholes in the northwestern part of Alachua County and from the southern part of Columbia County, Florida. Juvenile specimens, from two sinkholes in Leon County are tentatively assigned to this species.[1]

Phylogenetic Trends

The entire concept of phylogeny rests on the assumption that from ancestral stocks, there have arisen, in time, the organisms that populate the Earth. Therefore the synthesis, or reconstruction, of the racial history of a group must entail at least a mental picture, regardless of how vague, of the characteristics of a member of the ancestral stock. Oftimes the fossil record will aid in bringing some of the characteristics into sharp focus and thus enable the student to depict those characteristics with less temerity. Most often, even with the aid of fossils, there are certain characteristics of this organism the nature of which must be postulated, so that a "hypothetical ancestor" is not a foreign concept to any student of evolution. For many groups of organisms the fossil record has been erased, or is so fragmentary as to be practically useless. Such is the case with the crayfishes of the Pictus Group. At the present no fossils of crayfishes related to the members of this Group are available. In the absence of the fossil record one must attempt to reconstruct from the maze of diversity existing in modern forms, an organism consisting of a combination of characteristics that appears to serve as a focal point from which the many lines of variation have diverged. Having no concrete evidence for the actual existence of any part of such an organism, the student is more reticent in presenting a concise description of this ancestor

[1] I wish to thank Mr. H. R. H. Heinemann of Florida State University for permitting me to include the records from Leon County.

than if there were a few fossils to give him some assurance that he was partially correct in his assumptions. Nevertheless, he must have reached certain conclusions concerning the ancestor even if all that is in clear focus in his mind are a few bristles!

For the purposes of the present discussion only four characteristics of the hypothetical ancestor of the Pictus Group are presented in "sharp focus": a broad, short areola (figure 3), a color pattern emphasizing a saddle (figure 3), and a gonopod (first pleopod) terminating in four distinct terminal elements (figure 13).

The Areola.—Although there are no experimental data available to support field observations that, in general, crayfishes with broad areolae are confined to lotic habitats, there seems to be little reason to doubt that as the length of the areola increases and the breadth decreases, there is a concomitant enlargement of the gill chamber. Regardless of the specific physiological effects, crayfishes with narrow, long areolae frequent both lentic and lotic habitats.

The members of the Pictus Subgroup have all retained a broad, short areola—ranging from 2.8 to 5.0 times as long as broad, and from 25.7 to about 30 per cent of the entire length of the carapace (Table 1). The members of the Seminolae Subgroup have, in general, somewhat narrower and longer areolae—ranging from 4.7 to 9.0 times as long as broad, and from 28.0 to 35.5 per cent of the entire length of the carapace. The narrowest and longest areolae encountered in the Pictus Group are in the members of the Lucifugus Subgroup where it is from 10.4 to 36.0 times as long as broad, and from 37.0 to 43.0 per cent of the entire length of the carapace. Thus, if the postulate that the generalized areola is a broad short one is tentatively accepted, it becomes obvious that the stream dwellers have retained the generalized type, the ubiquitous members a somewhat intermediate type areola, and that the extreme types are to be found in the members frequenting subterranean habitats.

The Rostrum.—Although there is a considerable degree of variation in the rostra of most of the species, and apparently some of the variation may be correlated with the type of habitat in which the crayfishes are found, there are certain types that may be generally associated with each species. It seems probable that all of the rostra have been derived from one in which the basal margins are parallel, become slightly convex, and again parallel to the base of the acumen where there is borne a pair of well developed

lateral spines. This type of rostrum is found frequently in *Procambarus pictus* and *Procambarus* sp. A, and occasionally in some of the other species of the Pictus Subgroup. Variations deviating from this type include rostra like those always found in *P. youngi* in which the margins are almost parallel from the base to the marginal spines, and in this species the acumen is as long as, or longer than, the remaining part of the rostrum. A third type of rostrum, in which the margins are parallel at the base but converge cephalically to the marginal spines, is found most frequently; in general, this convergence is most extreme in the members of the Seminolae Subgroup where in some animals the marginal spines are entirely lacking, and there is scarcely to be found an emargination delimiting the base of the acumen. It is of interest that in the Lucifugus Subgroup, the rostrum of *P. lucifugus lucifugus* is remarkably like that of the generalized type in that the margins are markedly convex; they are less so in *P. lucifugus alachua,* and in *P. pallidus* they are almost always markedly convergent.

Among the members of the three subgroups it may be seen that the more generalized rostrum is found in the Pictus and Lucifugus subgroups and that the extreme type is more typical of the members of the Seminolae subgroup; however, it should be emphasized that occasional specimens of *P. seminolae* and *P.* sp. D have rostra that more nearly approach the generalized type than do some specimens of *P. enoplosternum, P. litosternum,* and *P.* sp. C.

The First Pleopod of the Male.—For many years it has been recognized that the complex structure of the first pleopod of the first form male affords the best single characteristic by which species of the genus *Procambarus* may be distinguished and at the same time point toward relationships between them. In the Pictus Group it seems probable that again we are forced to rely heavily on resemblances and differences observed in this appendage for the more detailed postulates concerning the evolution of the several species. Whereas it seems highly probable that the invasions of various types of habitats have been possible only when certain modifications in the areolae and rostra of the crayfishes were accomplished, there is no evidence to indicate that a reorganization of the pleopod was involved. Certainly there are no generalizations that have been recognized that tend to correlate a certain type of pleopod with a particular type of habitat. Thus, in attempting to reconstruct adaptive radiation in this group, if there is no evidence

among crayfishes in general that certain pleopod types may be correlated with certain environments, it seems probable that its use as a yardstick to measure relationships would be more reliable than other characteristics that reflect in part, at least, the habitat in which the animal lives.

An analysis of the pleopods of all the species of the Pictus Group has resulted in the postulate that the most generalized pleopod, and consequently that which probably should be considered to approach that of the hypothetical ancestor of the group, is that of *Procambarus pictus* and *Procambarus* sp. A. Rather than becoming involved in a long, detailed, verbal account of the relationships indicated by a comparison of the pleopods of the species concerned, figures 5 through 20 have been included. Lines have been drawn between them to indicate postulated affinities of all the species of the group. For orientation in attempting to recognize homologous terminal elements, it is suggested that the *central projection*, consisting in each instance of two closely applied parts, be used as a focal point.

The major trends in the evolution of the first pleopod appear to have been (1) in a reduction and loss of the caudal element. In all of the species of the Pictus Subgroup, except *P. youngi* and *P.* sp. B, the caudal process is present in the form of a small corneous tooth. It is absent in the two species just mentioned and in all of the species assigned to the Seminolae and Lucifugus subgroups. (2) Another trend has been in the suppression of the shoulder on the cephalic margin of the appendage. While it was impossible to illustrate adequately this in figures 5 through 20, the shoulder is best developed in *P. pictus*, somewhat less well developed in *P. enoplosternum* and *P.* sp. A; it is folded mesially, represented by vestiges, or is absent in the others. (3) The *cephalic process* which somewhat hoods the central projection in the more generalized forms appears to have become more spine-like in the members of the Seminolae Subgroup and in *P. youngi*, *P. pubescens*, and *P.* sp. B, and in *P. lepidodactylus* it has assumed a position lateral to the central projection.

Color Pattern.—The color pattern that is found in *Procambarus pictus* appears to be as generalized as that of any member of the group, and is illustrated in figures 1 and 3. A detailed description of this is beyond the scope of the present discussion, and only the "saddle" marking is given attention here. For simplicity in dis-

cussion it is considered to consist of a posterior *bar* which extends across the caudal margin of the carapace and the two forward-projecting lateral *horns*. In *P. pictus* this saddle is complete: the bar has a slight median emargination, and its ventrolateral terminii are continuous with the paired horns that extend cephalically to the cervical groove. While there is slight variation in *P. pictus* in the depth of the median emargination on the bar so that it is occasionally bisected, the general pattern is that represented in the figures indicated above. This pattern is most closely approached by *P. youngi* and *P.* sp. A; however, the lateral horns do not extend forward to the cervical groove, and the bar is usually broken on the median line. The bar and the two lateral pairs of dark spots representing the anterior and posterior portions of the horn are present in *P. enoplosternum*, *P.* sp. C, *P. pubescens*, and *P. hirsutus*. In some specimens of all of these the two dark spots may be connected by a band that is somewhat diffuse and paler in color. In *P. lepidodactylus* the lateral spots are not always present, but the broken bar is always evident. In *P. lunzi* and *P.* sp. D the bar is lacking, but the paired horns are complete (figure 2). In *P. seminolae* the bar is lacking and the horns are represented by two pairs of lateral spots (figure 4) corresponding to the anterior and posterior portions of each horn.

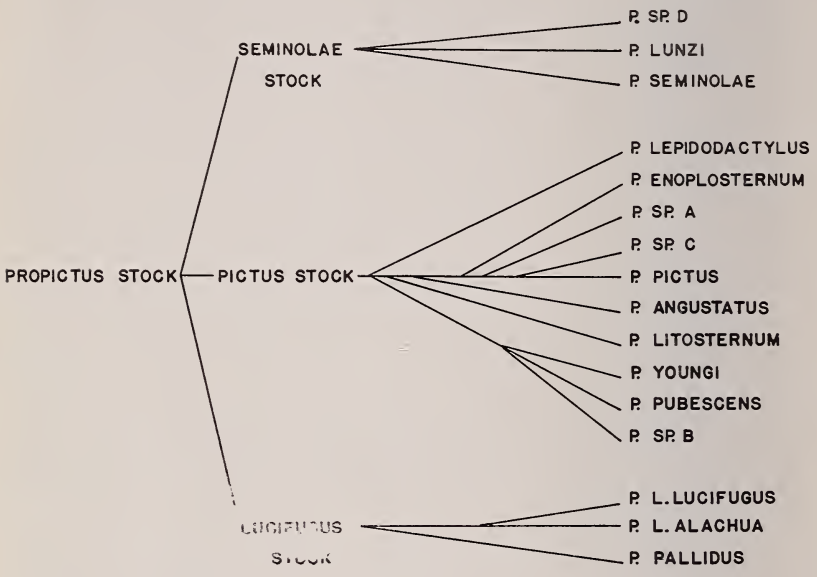
It seems apparent that the trend in variation insofar as the pattern of the saddle is concerned is toward its obliteration; however, only in the albinistic forms has it been completely eliminated. Extreme reduction is seen in *P. seminolae* which has only the two pairs of lateral spots (portions of the horns) and in *P. lepidodactylus* which has two segments of the bar. That these so-call remnants are actually homologous to portions of the saddle can scarcely be denied when specimens of all of the species are compared and almost a complete series of intermediate patterns are noted.

History of the Pictus Group

On the basis of these data, and others that are not presented here, the following diagram has been executed to depict the interrelationships of the members of the Pictus Group.

Although it is highly probable that much of the evolutionary history of the Pictus Group was accomplished during the Pleistocene Period, the invasion of the freshwaters of the area that is now with-

in the boundaries of the Piedmont Province by freshwater crayfishes must have occurred during the late Cretaceous or perhaps during the Tertiary. As has been stated above, the lack of fossils prohibits any accurate temporal assignments in the evolutionary history of the group.



It is postulated that the Propictus Stock had gained a foothold in at least some of the streams of the southeast not later than the Pliocene—probably much earlier—and that their migrations from one river system to another were largely dependent upon stream piracy or short migrations across very narrow land barriers between the dove-tailing headwaters of adjacent drainage systems. (This assumption is made because none of the modern species thought to be similar to the ancestral stock has been found on land or in ponds, lakes, or any other type of lentic habitat.) In this manner the stock invaded most of the major systems in the area between the Pee Dee River in South Carolina and the Altamaha River in Georgia, and during the middle Pliocene when "the Gulf of Mexico extended farther to the north than now, and Florida was a short, stubby peninsula that ended at about the level of Tampa . . . " (Hubbell, 1954 : 46) the stock gained an entrance into the peninsula. Almost certainly by this time the porous Eocene lime-

stone underlying the eastern portion of the peninsula had begun to be honeycombed and there was developing a system of subterranean pools and streams. There is no reason to doubt that some of the surface waters were being deflected from their coastal routes into these subterranean channels, just as is the case at the present time. Certainly such a setting was at least conducive to the invasion of these hypogean waters by members of the stream-dwelling Propictus Stock, and it is postulated that in taking advantage of this opportunity this Stock successfully invaded these waters—perhaps in two areas. In the southern area either two already differentiated stocks independently entered the underground waters, which seems most probable, or there was a subsequent marked dicotomous divergence in members of a single stock, resulting subsequently in the evolution of the sympatric *Troglocambarus maclanei* and *Procambarus lucifugus,* the latter consisting of two geographic races. The second (or third) invasion of the subterranean waters must have occurred farther to the north, this one representing the ancestral stock of *P. pallidus.* The presence of these troglodyte species in the subterranean waters of Florida almost demands an assumed insular land mass throughout the Pleistocene. Hubbell's (loc. cit., p. 48) statements regarding insular Florida are particularly apropos. "Not so long ago the geologists would have none of this [land in central Florida since the Pliocene] at least for the highest Pleistocene level of the sea, but in his latest maps Cooke has left a tiny island exposed just about where it is needed. If it were only a little larger!" In this I heartily concur!

The question arises as to what became of the original surface stock from which the cavernicoles took their origin. Only a small fragment of it is to be found in Florida at the present time—the relict, *P. pictus.* This species, presumably the one most closely approximating the ancestral stock of the group, has been found in only one stream tributary of the St. Johns River in northeastern Florida. Geographically disjunct in relation to its epigean relatives, its presence here can be explained only by the assumption that it is a relict form left on an insular landmass that persisted throughout the submergences of the landmass to the north during the Pleistocene. In support of this hypothesis, it is remarkable that in northeastern Florida Cooke left a sizable island in precisely the right place for the ancestral *P. pictus* to have persisted, and the creek in which it now occurs lies largely within an area of the

Duplin marle, an exposed Miocene formation, apparently occupying the cite of Cooke's island!

Perhaps to be correlated with the developing coastal plain during the Pleistocene is speciation in the Seminolae Stock. Almost certainly there was an offshoot of the Propictus Stock—a segment that ventured into lentic habitats. There is considerable evidence that this was one of the most important events in the evolution of the crayfishes of this genus, for it seems highly possible that the Blandingii Group, one of the largest of the genus, had its origin in this Seminolae Stock. Disregarding the importance of this stock except as it pertains to the Pictus Group, it is postulated that it had its origin in the area between the Santee and Altamaha rivers late in the Pliocene and that with the emergence of the low-lying coastal plain from the ocean during the Pleistocene, the developing ponds and swamps were rapidly invaded by these animals. Not only could they tolerate lentic habitats but also were able to occupy land on which the water table was attainable through their burrowing prowess. The three extant species of this group, assumed to have originated from the Seminolae Stock, present a tantalizing problem in attempting to decipher which most closely approximates the ancestral stock. In rostral characteristics *P. seminolae* and *P.* sp. D. share the honor; the areola of *seminolae* is the broadest and shortest; in color pattern *lunzi* and sp. D are more generalized; and the first pleopod of *lunzi* seems to be more primitive. Thus, until more data are available on these species, or additional related living or fossil forms are discovered, no detailed hypothesis concerning their inter-relationships can creditably be proposed. Of interest in relation to the distribution of the members of this subgroup is the apparent small range of *P. lunzi* and the absence of a representative of the subgroup in the area between the Savannah and Altamaha rivers. One is tempted to explain these two observations by calling on competition with one or more other species—in these situations the eastern red swamp crayfish, *P. troglodytes,* the range of which extends from the Altamaha River northward in the coastal plain to the Pee Dee River system.

Within the Pictus Subgroup, each species is largely confined to a single or adjacent river systems, and except for the streams in the area between the Altamaha, St. Johns, and St. Marks rivers, most of the lotic habitats from the Pee Dee River to the Chipola River in Florida are inhabited by one or more species of the sub-

group. As stated above, the single species which is thought to approximate most closely the ancestral stock is the geographically disjunct *P. pictus,* and a possible explanation of its presence in the St. Johns drainage is presented. The only other geographically disjunct species of the subgroup is *P. youngi* which is known from only three localities in the panhandle of Florida.

If it may be assumed that during the Pliocene the Propictus Stock had gained entrance to the major drainage systems from the Pee Dee River southward to Florida, then few postulates are necessary to synthesize a plausible explanation of the evolution of the stream-dwelling descendants of the stock. (1) In the Pee Dee system a marked divergence from the ancestral pattern was soon developed; this is seen in a number of characteristics, among the most obvious of which was the lateral shifting of the cephalic process of the first pleopod of the male (c.f. figures 10 and 13), and from this stock arose *P. lepidodactylus* which probably much later made its way southward into eastern tributaries of the Wateree (Santee system) River. (2) Another marked alteration arose in the stock, here termed the Pubescens Stock, that found its way into the Edisto, Salkehatchie, and Savannah river systems. One of the most conspicuous changes in this group was the loss of the caudal element of the first pleopod of the male (c.f. figures 8, 9, 11 and 13). It is believed that this occurred during the Pliocene and that descendants of this stock reached a tributary of the Apalachicola River, presumably a tributary of the Flint River. With the inundation of much of the coastal plain during Brandywine (early Pleistocene) times, the now three (or more) stream-dwelling derivatives of the old Propictus Stock suffered a severe setback, for except for the insular forms that were able to survive in the area of the Florida peninsula, all of those crayfishes living below the present 270 foot contour perished. With the subsequent retreat of the seas from the coastal plain during the Pleistocene and the accompanying extensions of old drainage systems, the three stocks reinvaded the once inundated area. Never again were any of them to cross southern Georgia, but the Pubescens Stock that had reached the Apalachicola system moved southward and invaded the three streams in the Florida panhandle in which *P. youngi* is now known to occur. Why its distribution is so limited is not known but suitable habitats are not numerous and it is found in an area in which there are a num-

ber of apparently very successful species. It is not inconceivable that this species is making its "last stand".

The remaining portion of the Pubescens Stock from which *P. youngi* took its origin was apparently separated into two parts, the more northern of which, occupying the Edisto drainage, gave rise to *P.* sp. B, and subsequently migrated into the younger Salkehatchie River, and eventually into a few eastern tributaries of the Savannah River. The other portion, occupying originally the Savannah drainage, gave rise to *P. pubescens* that invaded the Ogeechee and tributaries of the Altamaha rivers.

In the more conservative Pictus Stock, the ancestors of *P. litosternum,* apparently early isolated in the Ogeechee River, had undergone such divergence that when other representatives of the stock later reached the system there was no opportunity for hybridization. It is thought that *P. litosternum* invaded the Newport system from the Ogeechee. A second invasion of the Ogeechee system by the conservative Pictus Stock and its subsequent divergence resulted in the origin of *P.* sp. C. In the Ohoopee River another segment of this conservative stock developed a tendency toward giantism which perhaps aided in the isolation of *P. enoplosternum.*

Elsewhere the Pictus Stock remained little changed and resulted in the widespread *P.* sp. A which at the present time is known from the Wateree, Congaree, Edisto, and Savannah rivers, and from isolated localities in the Ogeechee and Ocmulgee rivers. It is of interest that this species so closely approaches the facies of *Procambarus pictus,* the species that has repeatedly been cited as that which probably most closely resembles the ancestral stock of the entire group.

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